

Allee Effects and Extinction in a Lattice Model

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Abstract

In the interest of conservation, the importance of having a large habitat available for a species is widely known. Here, we introduce a lattice-based model for a population and look at the importance of fluctuations as well as that of the population density, particularly with respect to Allee effects. We examine the model analytically and by Monte Carlo simulations and find that, while the size of the habitat is important, there exists a critical population density below which extinction is assured. This has large consequences with respect to conservation, especially in the design of habitats and for populations whose density has become small. In particular, we find that the probability of survival for small populations can be increased by a reduction in the size of the habitat and show that there exists an optimal size reduction.

Key words: Extinction; Allee effects; Critical population density; Habitat size; Fluctuations; Mean field; Monte Carlo simulations

1. Introduction

Extinction is becoming a greater and greater issue all over the world and is a cause of extreme concern. It has been estimated that anthropogenic extinctions are resulting in the loss of a few percent of the current world's biosphere, which is of magnitude 3 to 4 times the natural background rate (May et al., 1995). The World Conservation Union (IUCN), through its Species Survival Commission (SCC) develops criteria to assess the extinction rate for plants and animals all over the world which enables them to keep a so-called *Red List* (www.redlist.org) of species which are threatened with extinction in order to promote their conservation. The list currently shows over 16,000 threatened species around the world - a 45% increase on the figure from the year 2000.

It has been shown by examining both discrete (Escudero, 2005) and continuous (Skellam, 1951) populations that, at least analytically speaking, there exists a critical habitat size L_c above which survival of a population is assured. Here we examine what role the population density plays since, intuitively, one would expect that even for $L > L_c$, a sufficiently large population would be needed for growth.

Lattice based models are widely used in ecology (see for example Tainaka, 1988; Durrett and Levin, 1998; Itoh et al., 2004) and so we introduce such a model that

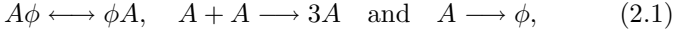
incorporates birth, death and diffusion. Unlike other similar models such as the *contact process* (e.g. Harris, 1974; Oborny et al., 2005), here two individuals must meet in order to reproduce whereas one individual can die by itself. This results in negative growth rates for populations that fall below a critical density due to reproduction opportunities becoming rare. In real populations, the positive correlation between size and per capita growth rate of a population is known as the Allee effect (Allee, 1931), which has recently received much interest (e.g. Dennis, 2002; Hurford et al., 2006; Johnson et al., 2006). If the Allee effect is strong enough, the population size may even decrease for small population sizes as in our model. Due to this behaviour, the effect has been examined with respect to extinction (see for example Amarasekare, 1998; Courchamp et al., 1999; Stephens et al., 1999, and references therein) but *primarily* deterministically and so without fluctuations in the population density. Since fluctuations are likely to be highly significant for small populations, we include the effects of these by examining Monte Carlo (MC) simulations in the hope to gain a more realistic picture of the importance of the population density on the chances of survival. Further to the stochastic methods used to study Allee effects, such as stochastic differential equations (e.g. Dennis, 1989), discrete-time Markov-chains (e.g. Allen et al., 2005) or diffusion processes (e.g. Dennis, 2002), lattice based models have space, as well as time, as a variable and take into account individuals, rather than just the macroscopic view of the population.

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After introducing the model in the next section, we examine the Allee effects present in our model in Section 3, particularly with respect to a sudden decrease in population in Section 5. The effects of the fluctuations are examined in Section 4.

2. The Model

We have a d -dimensional square lattice of linear length L where each site is either occupied by a single particle (1) or is empty (0). A site is chosen at random. If the site is occupied, the particle is removed with probability p_d , leaving the site empty. If the particle does not die, a nearest neighbour site is randomly chosen. If the neighbouring site is empty, the particle moves to that site. If however the neighbouring site is occupied, with probability p_b ¹, the particle reproduces, producing a new particle on another randomly selected neighbouring site, conditional on that chosen square being empty. We therefore have the following reactions for a particle A :



where ϕ represents an empty site. A time step is defined as the number of lattice sites and so is equal to approximately one update per site. We use nearest neighbours and, throughout most of the paper, periodic boundary conditions which, although more unrealistic than, say, reflective boundary conditions, allow for better comparison with analytical results, since periodic systems remain homogeneous. We later, however, examine some results with reflective boundary conditions.

Due to the conflict between the growth and decay processes in the model, we expect that with certain values of p_b and p_d , extinction of the population would occur. Indeed, many models displaying such a conflict (see for example Vespignani et al., 2000; Dammer and Hinrichsen, 2003; Oborny et al., 2005; Peters and Neelin, 2006) show a critical parameter value separating an *active* state and an *inactive* or *absorbing* state that, once reached, the system cannot leave. As the rate of decay increases, the so-called *order parameter* (often the density of active sites) decreases, becoming zero at a critical point, marking a change in phase or *phase transition*. In our case, the absorbing state would represent an empty lattice and so extinction of the population.

To show that this is indeed the case for our model, we derive a so-called mean field equation (e.g. Oppen and Saad, 2001) for the density of occupied sites $\rho(t)$. Assuming the particles are spaced homogeneously in an infinite system we have

$$\frac{\partial \rho(t)}{\partial t} = p_b(1 - p_d)\rho(t)^2(1 - \rho(t)) - p_d\rho(t). \quad (2.2)$$

¹ We note that the birth rate is actually given by $p_b(1 - p_d)$ and not p_b only.

The first term is the proliferation term and so is proportional to ρ^2 , the probability that the particle does not die ($1 - p_d$), the probability that the next randomly chosen site to give birth on is empty ($1 - \rho$) and finally the probability that it gives birth if this is the case, p_b . The second term represents particle annihilation and so is proportional to both ρ and p_d , the probability that the chosen particle dies.

Eq. (2.2) has three steady states,

$$\bar{\rho}_0 = 0, \quad \bar{\rho}_{\pm} = \frac{1}{2} \left(1 \pm \sqrt{1 - \frac{4p_d}{p_b(1 - p_d)}} \right). \quad (2.3)$$

For $4p_d > p_b(1 - p_d)$, $\bar{\rho}_{\pm}$ are imaginary, resulting in $\bar{\rho}_0$ being the only real stationary state and so, here, extinction occurs in all circumstances. Keeping p_b a constant from now on, we then have that our critical death rate is given by $p_{d_c} = p_b/(4 + p_b)$ which separates the active phase representing survival and the absorbing state of extinction.

Clearly Eq. (2.2) is limited by the exclusion of diffusion and noise as well as the false assumption of a homogenous population density. We do however find at least good qualitative support for our mean field analysis through numerical simulations. Fig. 1 a) shows the critical values of p_d and p_b separating the regions with one and three stationary states according to both the mean field equation and numerical simulations for 1, 2 and 3 dimensions. We see convincing agreement between our analytical and numerical results, particularly for higher dimensions. The MC simulations were carried out on an initially fully occupied lattice with linear sizes $L = 1000, 32$ and 10 for each dimension respectively and we observed whether extinction occurred during 10^5 time steps. For each birth rate, the simulation was repeated 500 times. If a single run survived, p_d was increased, whereas if extinction occurred in all runs, p_d was reduced. Using the same initial seed for the random number generator, an iterative procedure produced a critical value with accuracy $\pm 2^{-11}$. This iterative procedure was then repeated 5 times with different seeds and the average taken. Only a small number of repeats were needed since the largest variance of the values obtained was of the order of 10^{-8} . From the figure we find that to 3 d.p. for $p_b = 0.5$, $p_{d_c} = 0.073, 0.098$ and 0.105 in 1, 2 and 3 dimensions respectively. Due to the finite size of the lattices and the finite time used for the above simulations, the actual critical death rates are likely to differ slightly from those given and more accurate techniques would have to be used to obtain them (see Hinrichsen, 2000, for examples of such techniques).

With $\rho(t = 0) = 1$, as p_d is increased, the steady-state population density decreases, becoming zero at p_{d_c} as shown in Fig. 1 b), marking the phase transition. We see that the steady state population density *appears* to change continuously in 1 dimension, whilst discontinuously in 2 and 3 dimensions in agreement with the mean field results. If indeed this is the case, we call such phase transitions *continuous* and *first-order* respectively. In both cases, the phase transition is marked by a very rapid decrease in

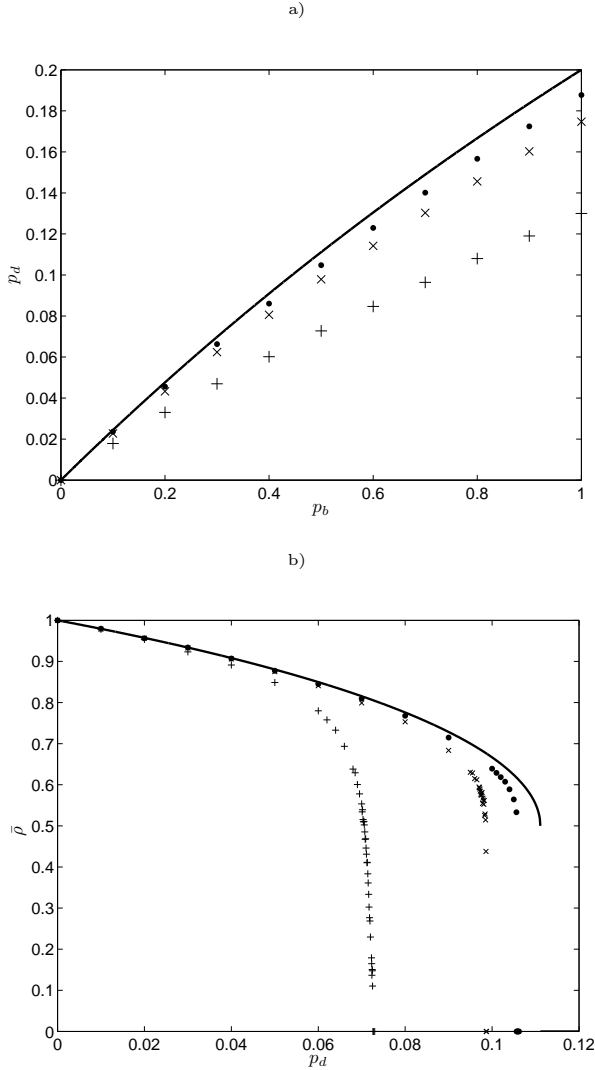


Fig. 1. a) Parameter domain for the number of steady states with the points showing the parameters giving 2 steady states and b) the steady state population densities with $p_b = 0.5$ for the mean field (line), 1 (+), 2 (x) and 3 (•) dimensional simulations.

population density.

Briefly relating our model to biology, we note that the death rate for a given species may fluctuate for any number of reasons but it must certainly be true that at least the average value of p_d must be less than p_{dc} for the species to have ever been in existence. However, as we have shown, even a temporary increase in p_d above p_{dc} , due to deforestation or disease for example, will cause a very rapid and perhaps unrecoverable decrease in population. Extinctions however may also occur for reasons other than having a super-critical death rate. We investigate the roles of Allee effects and that of fluctuations in the next three sections where we examine simulations in the sub-critical or active phase and use the constant value $p_b = 0.5$.

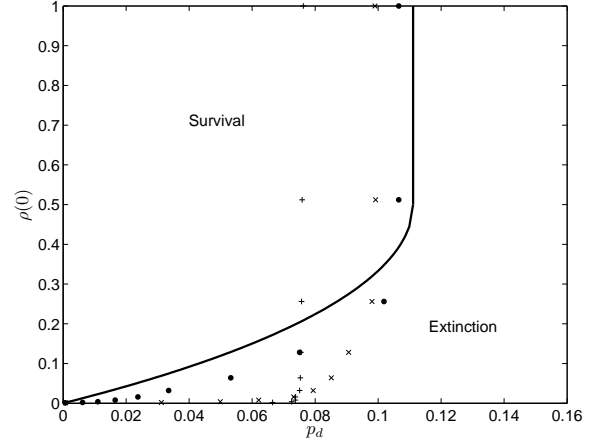


Fig. 2. Phase diagram showing the critical values of p_d separating the 2 long-term outcomes of the system for different initial population density according to the mean field (line) and the 1 (+), 2 (x) and 3 (•) dimensional MC simulations.

3. Allee Effects

One reason we observe a decline in population growth at low densities is due to individuals finding it harder to find a mate. This is empirically known to occur in both plant (e.g. Aizen and Feinsinger, 1994) and animal (e.g. Lande, 1987) populations. In our model, this aspect is incorporated by the fact that two individuals are required for reproduction whereas an individual can die by itself. As density decreases, each individual therefore finds it increasingly difficult to find another for reproduction before they die. To examine this, we return to our mean field equation (2.2).

It is easy to show that whereas $\bar{\rho}_+$ and $\bar{\rho}_0$ are stable stationary points of Eq. (2.2), $\bar{\rho}_-$ is unstable. Since in the active phase, $\bar{\rho}_0 < \bar{\rho}_- < \bar{\rho}_+$, any population whose density $\rho(t) < \bar{\rho}_-$ will be driven to extinction by the dynamics of the system. In fact we find that for $p_d < p_{dc}$,

$$\rho(t) \longrightarrow \begin{cases} 0 & \text{for } \rho(t) < \bar{\rho}_- \\ \bar{\rho}_+ & \text{for } \rho(t) > \bar{\rho}_- \end{cases} \quad \text{as } t \longrightarrow \infty. \quad (3.1)$$

We test this numerically in 1, 2 and 3 spatial dimensions by finding the value of p_d that separates the active and absorbing states for different initial conditions. The MC simulations were carried out and the critical death rate found iteratively in the same fashion as in Section 2. The results are shown in Fig. 2 and clearly show the importance of the initial population density for survival. The density dependence appears to increase with dimensionality, which we expect, since two individuals meeting becomes progressively harder as the dimensionality of the system increases.

The existence of this critical population density is highly significant to the conservation of species. It is clear that a sufficiently small population will not grow, regardless of how much space and resources are available. It also has repercussions if a population density were to suddenly decrease due to disease or particularly harsh meteorological

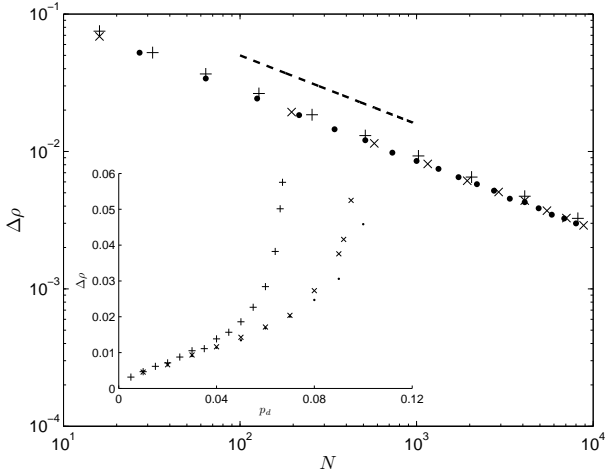


Fig. 3. Log-log plot of the standard deviation of the population density versus the number of sites in the 1 (+), 2 (x) and 3 (•) dimensional systems. The hashed line has gradient -0.5 for the eye and indicates the power law behaviour. Insert: The fluctuations v.s. p_d dimensional case with the same symbol notation.

conditions, for example. We examine this further in Section 5 after examining the role of fluctuations.

4. Fluctuations

We expect extinction due to fluctuations in the population density to occur when the order of the fluctuations approaches the mean population density. Empirically, demographic stochasticity (that is, chance events of mortality and reproduction) is known to be greater in smaller populations (Lande et al., 2003) than in larger ones. Population and habitat size are, on average, positively correlated and so, particularly with the existence of the critical population density, we expect extinction due to fluctuations to occur for smaller lattice sizes as has been suggested by others (e.g. Pimm, 1991; Escudero et al., 2004).

We see in Fig. 3 that, numerically, the fluctuations in the population density $\Delta\rho$ decrease with the number of lattice sites N through a power law with exponent -0.50 in all dimensions, which is what we would expect from the *central limit theorem*. Simulations were carried out for fixed $p_d = 0.03$ and $p_b = 0.5$ and the standard deviation obtained from 5×10^3 surviving runs for each lattice size. The insert in Fig. 3 shows how the size of the fluctuations also increase as the critical point is approached. These larger fluctuations will also increase the probability of extinction as indicated in Fig. 4 where we examine the probability of survival P_s , that is, the probability that extinction has not occurred up to some time t_m . We examine the 1 dimensional case only using three different values of p_d with $t_m = 10^3$ and repeat the simulation 5×10^4 times for each lattice size. The figures clearly show how the probability of survival increases with L , yet decreases as p_d increases. Indeed, as p_{dc} is approached, population density decreases and fluctuation size increases resulting in species with higher death rates be-

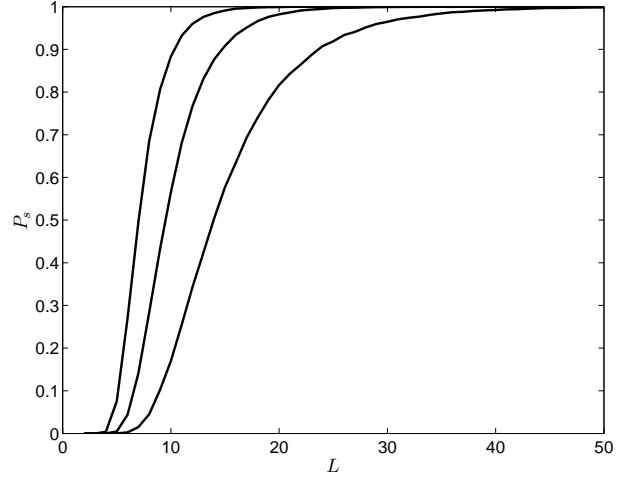


Fig. 4. How P_s varies with L for the 1 dimensional model with (from left to right), $p_d = 0.04, 0.05$ and 0.06 . Similar results are seen in 2 and 3 dimensions.

ing more susceptible to extinction. This is indeed observed in nature where long-lived species are known, in general, to have a higher chance of survival than short-lived ones (Pimm, 1991).

5. A Decrease in Population Density

Apart from the initial conditions, it is certainly conceivable that the population density could fall below the critical value due to a reduction in population size. From Eq. (3.1) we expect that the population will survive only as long as $\rho(t) > \rho_c$. We simulate this by increasing p_d to 1 at some $t = t_k$ and then returning p_d to what it was before, once a density ρ_s has been reached. We examine this here in 2 dimensions with now reflective rather than the previously used periodic boundary conditions. Qualitatively, all previous results have been very similar when using reflective boundary conditions but here we want to increase this degree of realism in our model.

For 2 dimensional simulations with an initial population density $\rho(0) = 0.128$, the critical death rate is 0.093 (3 d.p.) as shown in Fig. 2. So, for $p_d = 0.093$, we would expect that if $\rho_s > 0.128$, the population will survive, with the population density returning to what it was before, whereas for $\rho_s < 0.128$, extinction will occur. Due to the fluctuations in the population that occur in the simulations, we expect more of an increase in the likelihood of extinction as $\rho \rightarrow \rho_c^+$ rather than the definite survival/extinction result that the mean field predicts. Fig. 5 shows the results for $\rho_s = 0.13$, where we see that for those runs that *did* survive, the population density does indeed return to what it once was. We also see, as expected, that most of the runs did result in extinction. In fact the survival rate was 0.004.

From Fig. 5 b) we observe that there is a time delay of approximately 40 time steps between the sudden decrease in population and when the survival probability begins to fall. Assuming a particle that dies the n th time it is picked,

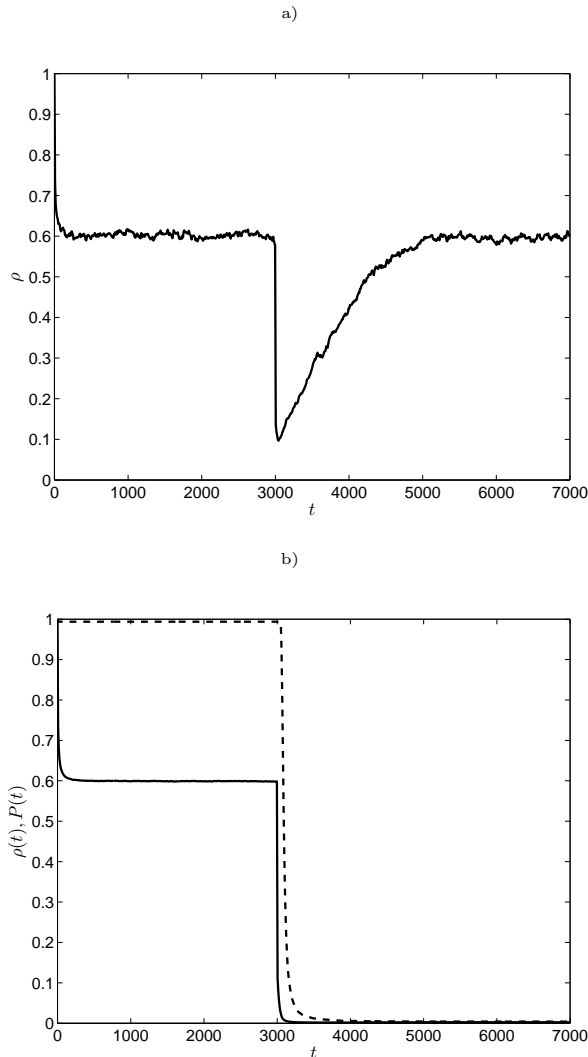


Fig. 5. a) The average population density of the surviving runs only. b) The average population density of all the runs (solid line) and the survival probability $P(t)$ (hashed line), i.e. the probability that extinction has not occurred up to time t .

survives $n-1$ time steps, it is easy to show that the expected lifetime (in time steps) of an individual is given by $(1 - p_d)/p_d$. We therefore have a time delay of approximately four lifetimes (recall $p_d = 0.093$) which, for a lot of species, is ample time to act.

In order to prevent extinction in such a case, the population density must be increased beyond ρ_c . This has important ecological implications since it shows that the probability of extinction can be decreased, not only by increasing the population (which is of course not always possible), but also by a *decrease* in habitat size.

To see whether this hypothesis holds, we simulate this again using $p_d = 0.093$ but this time $\rho_s = \rho_c = 0.128$ so that the chance of survival is negligible. This time however, once the population density has been reduced, the area covered by the lattice is reduced by half. The organisms in the half that remains are left where they are, whereas those in the half that is removed are randomly placed in the

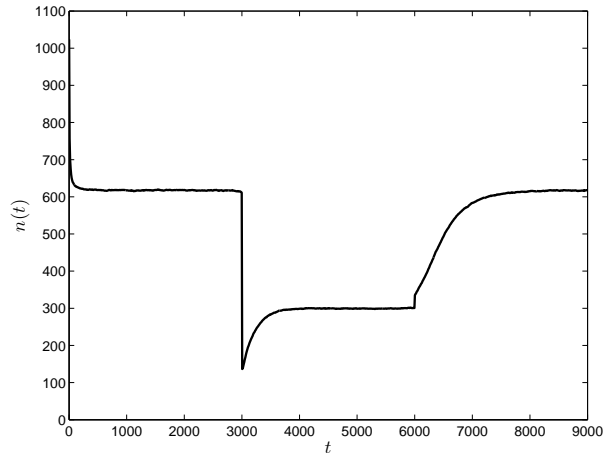


Fig. 6. Plot showing the recovery of the population $n(t)$ for the surviving runs only after a disease breakout at $t = 3000$ due to the re-sizing of the lattice. The lattice is returned to how it was originally at $t = 6000$ and the population recovers its original value.

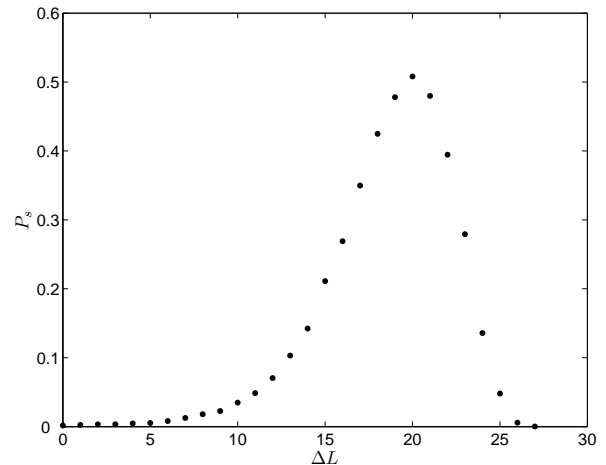


Fig. 7. How the probability of survival changes with different reductions in L , starting from $L = 32$.

remaining half. This then doubles the population density, bringing the population out of the sub-critical population density. Once the population has recovered and stabilised, the lattice size is returned to how it once was. The results are shown in Fig. 6 and clearly show the recovery of the population once the lattice size has been reduced. In fact, out of 1000 runs, the probability of survival rose from 0.003 to 0.281.

We expect there to be an optimal habitat reduction size - too large a reduction and the population will be in danger from large fluctuations associated with smaller habitat sizes whereas too small a reduction and the density will not be increased sufficiently. We therefore plot in Fig. 7 the probability that the system does not go extinct up to some $t = t_{max}$, P_s , against the reduction in L , ΔL . We again use $p_d = 0.093$ and $\rho_s = 0.128$. For small ΔL , P_s changes little due to the density not being reduced enough, yet for larger ΔL , the larger fluctuations resulting from the smaller value

of L also cause P_s to be small.

Whilst reflective boundary conditions were used here, very similar results were obtained using periodic boundary conditions. In fact, with periodic boundary conditions, the probability of survival increased more significantly by the decrease in L due to the population being able to grow in two directions rather than in just one after the habitat size has been returned to what it once was. This of course could be achieved in reality by reducing the habitat from more than one direction.

This model was proposed to represent how the area in which a population is found could be reduced in real-life. The species could be driven towards one end of the habitat with a boundary placed to prevent them leaving the desired area. This boundary could then be removed once the population has recovered. Clearly this is easier for larger, land-based animals but in principle, at least, could be achieved for all species.

6. Conclusions

Allee effects are certainly observed in nature (Stephens and Sutherland, 1999; Pedersen et al., 2001; Gyllenberg et al., 1997, et al) and have been studied with respect to extinction. Using a lattice model, we have observed Allee effects together with the role of fluctuations, with the advantage of being able to examine the effects of habitat size. Being able to model the population as a group of *individuals* which move, breed and die, rather than as a variable in an equation, has enabled us to gain a more realistic insight into how real populations behave.

Rather than the clear-cut conclusions that deterministic models produce, conservationists often examine the *probability* that a population will maintain itself without significant demographic or genetic manipulation for the foreseeable ecological future (Soulé, 1987). In this spirit, for a sufficiently large population density we have shown that the probability of survival does increase with habitat size due to the smaller fluctuations. However, far more important are the death rate and population density since if these fall on the wrong side of their critical values, extinction is almost a certainty.

Our findings are certainly significant for the design of habitats. The notion of a critical habitat size, mentioned in the Introduction, is misleading, since, it is certainly not true that for a fixed population size, the larger the habitat size the better. Regardless of the amount of space and resources available, a population will only grow if the density is above its critical value. We also proposed, in the last section, a method for greatly reducing the probability of extinction by reducing the habitat size once a species has become rare.

Our notion of density has been that of the number of individuals per unit area. While we assumed this to be constant in space when deriving our mean field equation (2.2), clearly this will vary amongst real populations. In

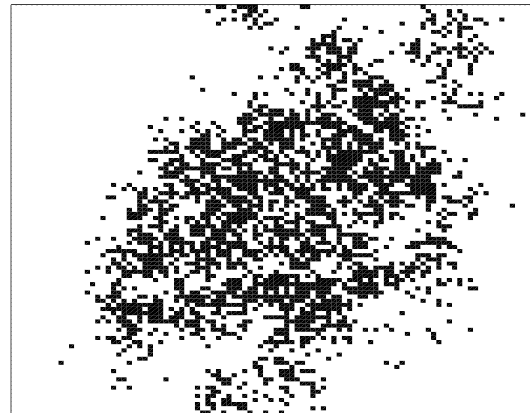


Fig. 8. Snapshot of the output from a 2 dimensional lattice with $L = 100$. A value of $p_d = 0.1$ was used and the picture was taken at $t = 600$ when $\rho = 0.2223$.

fact, for populations that are found in patches, the value of the density will depend very much on the scales used. The same is true of the MC results as shown in Figure 8, where we see clear examples of clustering. In nature, species will cluster to varying degrees and hence the value of the critical population density will also vary and would need to be estimated in each case.

Compared to other stochastic models, we claim the use of lattice models gives a more realistic insight into the way in which real populations behave. We do still however, recognise the inaccuracies in our model and the difficulties in implementing the observations. We believe the model to be valid, to a greater or lesser degree to all species which rely on others for growth, perhaps particularly those who live alone yet sexually reproduce. In fact, due to the great variety of species, we have presented the above as ideas which may be of qualitative, rather than quantitative, relevance to conservation management.

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